NIMBADON, A NEW GENUS AND THREE NEW SPECIES OF TERTIARY ZYGOMATURINES (MARSUPIALIA: DIPROTODONTIDAE) FROM NORTHERN AUSTRALIA, WITH A REASSESSMENT OF *NEOHELOS*

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Three new species of Oligo-Miocene zygomaturine diprotodontids are described from northern Australia. All are small, plesiomorphic and appear to comprise a distinctive clade of zygomaturines, named here *Nimbadon*. The clade is partly defined on the basis of the posteriorly inclined P^3 parastyle and blade extending from the parametacone to the lingual half of the P^3 crown and then to the anterolingual cingulum. Two of the species are known from Oligo-Miocene local faunas of Riversleigh Station, northwestern Queensland. The third is from the middle Miocene Bullock Creek Local Fauna of Camfield Station, northwestern Northern Territory. Description of additional fossil material referable to *Neohelos tirarensis* Stirton, 1967, a middle Miocene zygomaturine from the Kutjamarpu Local Fauna of South Australia, enables the genus to be distinguished from *Nimbadon*. The chronostratigraphic significance of the new zygomaturines is considered and found to approximately correspond to current understanding of the relative ages of the deposits from which the specimens were obtained. ☐ *Diprotodontidae, Zygomaturinae, Nimbadon, Neohelos, Oligo-Miocene, Riversleigh, Bullock Creek Local Fauna, Henk's Hollow Local Fauna, Fig Tree Local Fauna.*

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Specimens representing a very small zygomaturine were collected between 1984 and 1986 by Archer, Godthelp and Hand from the Henk's Hollow Site, in an as yet unnamed freshwater limestone on the Gag Plateau of Riversleigh Station (Archer, Hand & Godthelp, 1986; Archer & Flannery, 1987; Archer et al., 1989, 1991). Referred material includes maxillary and dentary fragments and isolated teeth. A second, larger Riversleigh species, represented by a maxilla, was collected in 1986 by Pledge from Fig Tree Site Locality adjacent to Godthelp Hill, Riversleigh Station.

A small Bullock Creek zygomaturine is known from a palate collected in 1981, by Rich and colleagues, from Horseshoe West Locality (WV 113) in the Camfield Beds of Camfield Station, northwestern Northern Territory (Rich et al., 1982, 1991).

Estimates of the age of the Henk's Hollow, Fig Tree and Bullock Creek Local Faunas are based mainly on stage-of-evolution comparisons of particular diprotodontian marsupials with those of other northern and central Australian faunas

(Rich et al., 1982, 1991; Archer & Flannery, 1983; Archer & Hand, 1984; Woodburne et al., 1985; Murray, 1990a; Murray & Megirian, 1990; Archer et al., 1989,1991). Recent reappraisal of the age of central Australian Tertiary mammalian faunas, based on the study of foraminifera (Lindsay, 1987), suggests that some of these faunas (e.g. the Ditjimanka, Pinpa and Ericmas Local Faunas) are appreciably older than once thought (e.g. Woodburne et al., 1985; but see Tedford, 1966), possibly late Oligocene. By comparison, the Bullock Creek Local Fauna is estimated to be ?middle Miocene in age, i.e. immediately post-Wipajiri (Murray, 1990a; Murray & Megirian, 1990). On-going studies (Archer et al., 1991) of the Riversleigh fossil faunas suggest that the Henk's Hollow Local Fauna is ?middle Miocene in age and the Fig Tree Local Fauna somewhere between late Oligocene and early Miocene in age.

The new zygomaturines described here are most similar to forms currently referred to the genus *Neohelos*. Their generic distinction, however, has been clarified by discovery at the type locality of new material referable to *Neohelos*

TABLE 1. Measurements of *Neohelos tirarensis* P^3 (AMF87625) and M^3 (AMF87626) from the Leaf Locality, Lake Ngapakaldi, South Australia. In mm. Abbreviations: ant, anterior; post, posterior; paramet, parametacone; protoc, protocone; parac, paracone.

P^3	Length	15.8
	width	13.9
	width(paramet to protoc tips)	5.5
	height(paramet)	11.4
	height(parastyle)	6.5
M^3	length	18.8
	width(ant)	17.2
	width(post)	15.8
	height(parac)	7.8

tirarensis, the type and only named species of the genus. The original description (Stirton, 1967) of this Miocene zygomaturine from the Kutjamarpu Local Fauna of central Australia was based on five isolated teeth collected in 1962 at the Leaf Locality, Lake Ngapakaldi, Etadunna Station, South Australia. The holotype, a broken P^3, preserves only the posterior portion of the tooth. Though less complete than the other teeth, it was selected as the holotype because of the importance of premolar morphology in diprotodontoid systematics (Stirton, 1967; Stirton, Woodburne & Plane, 1967).

In 1982 two isolated teeth referable to *N. tirarensis* were collected from the type locality by Archer, Hand, T. Flannery, G. Hickie, J. Case and P. Bridge: a well-preserved RP^3 (AMF87625) and RM^3 (AMF87626). These add considerably to knowledge of this species. Additional materials referable to *Neohelos* from the Bullock Creek Local Fauna (Plane & Gatehouse, 1968; Plane, 1971; Murray & Megirian, 1992) and various Oligo-Miocene Riversleigh local faunas (Archer et al., 1989, 1991) are presently under study.

Institutional abbreviations used here are as follows: QMF, fossil collection of the Queensland Museum; AMF, fossil collection of the Australian Museum; SAMP, palaeontological collection of the South Australian Museum; NMVP, palaeontological collection of the Museum of Victoria; AR, research collection of the School of Biological Sciences, University of New South Wales. Cusp nomenclature follows Archer (1984) and Rich, Archer & Tedford (1978). The posterolingual cusp of the upper molars, conventionally called the hypocone (e.g. Stirton, Woodburne & Plane, 1967), is now called the metaconule following Tedford & Woodburne (1987) but the posterolingual cusp of P^3, follow-

ing unchallenged convention, is called the hypocone. Cheektooth homology is that proposed by Archer (1978). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATICS

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Family DIPROTODONTIDAE Gill, 1872
Subfamily ZYGOMATURINAE Stirton,
Woodburne & Plane, 1967

Neohelos Stirton, 1967
(Fig. 1, Table 1)

Type species. Neohelos tirarensis Stirton, 1967

REVISED GENERIC DIAGNOSIS
The following combination of features appears to distinguish species of *Neohelos* from all other zygomaturines: P^3 with large, erect parastyle that is well isolated from the parametacone; parastyle is conical without tip developed as a blade; anterolingual basin well defined in P^3 by distinct basal cingulum extending between parastylar corner of tooth to anterolingual base of protocone; P^3 parametacone with an undivided tip; parametacone tip not developed into anterobucally oriented blade; line between protocone, parametacone and widest buccal point on crown is approximately rectilinear and divides crown either in half or leaves anterior division shorter than the posterior division; P^3 with well-developed hypocone or hypocone shelf; M^{2-3} with well developed parastyle and metastyle.

Nimbadon n.gen.
(Figs 2-5, Table 2)

Type species. Nimbadon lavarackorum n.sp.
Additional species. Nimbadon whitelawi n.sp., *Nimbadon scottorrorum* n.sp.

GENERIC DIAGNOSIS
Species of *Nimbadon* differ from those of all other zygomaturines (with special reference to *Neohelos*, the taxon to which they are otherwise most similar) in the following combination of features: small size (although they are larger than *Raemeotherium* Rich, Archer & Tedford, 1978); in having a molar gradient that does not appreciably increase postcriorly (in contrast to all other zygomaturines except *Raemeotherium*); posteriorly inclined parastyle on P^3 (rather than conical
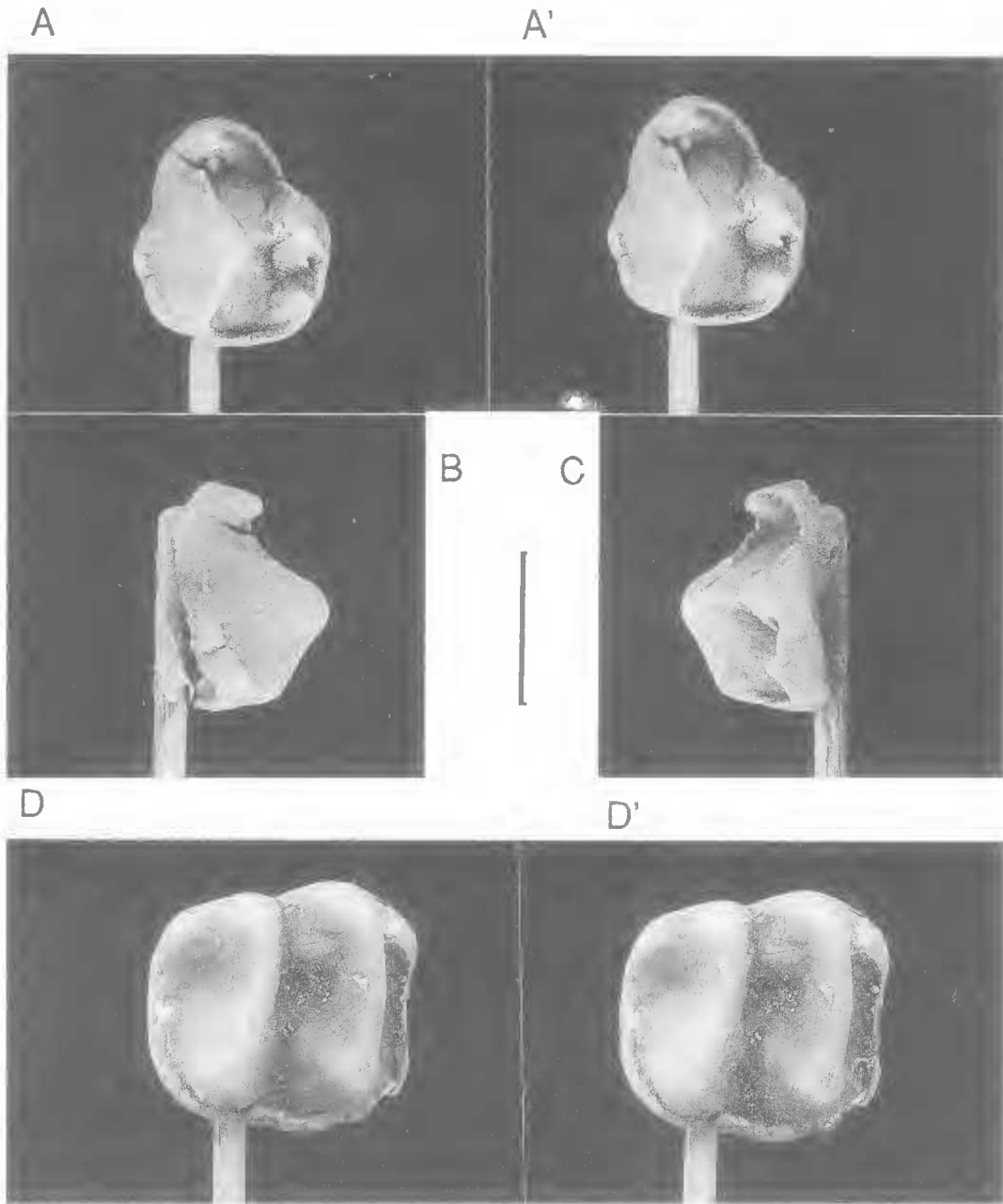
FIG. 1. *Neohelos tirarensis*, Leaf Locality, Lake Ngapakaldi, South Australia. AMF87625, RP^3: A-A', occlusal stereopair; B, buccal view; C, lingual view. AMF87626, RM^3: D-D', occlusal stereopair. Bar indicates 10mm.

and erect as in other zygomaturines except possibly *Plaisiodon centralis* Woodburne, 1967); an anterolingual blade on the parastyle of P^3 that surmounts a posterolingually oriented thegotic facette (in contrast to no apical blade such as may[?] characterise *Neohelos*); completely undivided parametacone on P^3 (in contrast to all other

zygomaturines except *Neohelos* and *Alkwertatherium* Murray, 1990b); an anterobuccal blade on the parametacone of P^3 that surmounts an obliquely oriented anterolingual thegotic faccte (in contrast to either no blade or a poorly developed anteriorly oriented blade such as may[?] characterise *Neohelos*); very small to absent hy-

TABLE 2. Measurements of *Nimbadon lavarackorum* n.sp., *N. whitelawi* n.sp. and *N. scottorrorum* n.sp. from Riversleigh and Camfield Stations, northern Australia. In mm. Brackets around figures indicate estimates. Abbreviations: ant, anterior; post, posterior; *Gag Site specimens.

LOWER DENTITION

Species		*Nimbadon lavarackorum*					
QMF		23142	23153	23154	23155*	23158	23159
P_3	L	12.5	10.9				
	w	7.0	5.8				
M_2	L	14.0		13.3	13.0		
	w(ant)	8.4		8.5	8.3		
	w(post)	9.4		8.6	8.4		
M_3	L	15.4					
	w(ant)	10.1					
	w(post)	10.0					
M_4	L	15.5				14.0	
	w(ant)	11.0				10.6	
	w(post)	10.2				9.8	
M_5	L	15.9					14.3
	w(ant)	11.1					11.2
	w(post)	10.0					9.9
P_3-M_5	L	72.7					
M_{2-5}	L	60.9					

UPPER DENTITION

Species		*Nimbadon lavarackorum*										*N. whitelawi* NVM P186506		*N. scottorrorum*
QMF		23141	23143	23144	23145	23146	23147	23148	23149	23150	23160*	right	left	23157
P^3	L	12.7	14.1	12.4								12.9	13.0	14.3
	w			10.3								(10.4)	10.9	13.4
M^2	L	11.9			13.3						14.1	13.1	13.2	17.1
	w(ant)	10.2			10.9						11.3	(9.3)		15.0
	w(post)	9.9			10.8						10.5	9.2		15.8
M^3	L	12.3					13.7				14.3	13.1		17.9
	w(ant)	11.3									11.6	10.9		
	w(post)	10.1					10.9				10.4	(9.5)		
M^4	L						13.8		14.3			13.5		18.5
	w(ant)						11.5		12.2			11.1		
	w(post)						10.7	12.5	10.4			9.7		
M^5	L									13.5				18.1
	w(ant)									11.3				
	w(post)									9.8				
Palate width												29.2		
P^3-M^5	L													(84.4)
P^3-M^4	L											52.8		66.3
P^3-M^2	L											25.3	25.8	48.2
M^{2-5}	L													(71.5)
M^{2-4}	L											39.5		53.1
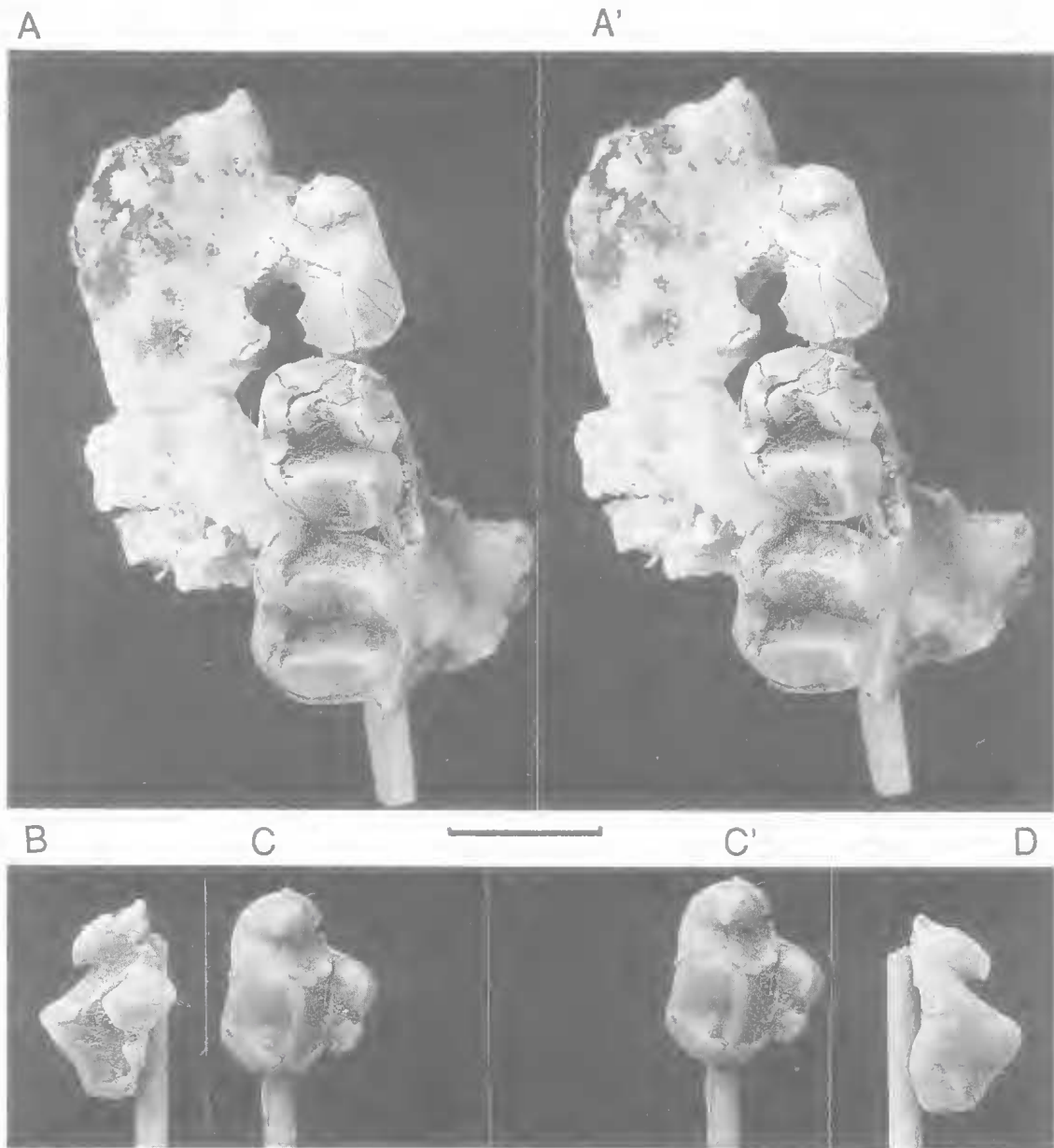
FIG. 2. *Nimbadon lavarackorum* n.gen., n.sp., Henk's Hollow Site, Riversleigh Station. A-A', QMF23141, holotype, left maxillary fragment with M^2, M^3 and buccal half of P^3, occlusal stereopair. B-D, QMF23143, RP^3: B, lingual view; C-C', occlusal stereopair; D, buccal view. Bar indicates 10mm.

pocone on P^3 (in contrast to *Alkwertatherium* and most but not all *Neohelos* and in contrast to all other zygomaturine P^3s where this cusp is large, including *Maokopia* Flannery, 1992); posterobuccal basal cingulum on P^3 (in contrast to most other zygomaturines except *Alkwertatherium* and *Neohelos* where this feature is variably

developed); poorly developed to absent anterolingual basal cingulum joining base of parastyle to base of protocone (in contrast to most other zygomaturines except some *Neohelos* where there may be only a very small cingulum); an anterolingual crest on P^3 that extends from the parametacone towards the protocone but, veering

anteriorly, bypasses the buccal crest from the protocone and extends to the anterolingual basal cingulum (in contrast to directly connecting to the buccal crest from the protocone as occurs in most if not all other zygomaturines); a line extended buccally through the protocone and parametacone passes anterior to the position of the widest point on the buccal base of the crown (in contrast to intersecting this point as it does in *Neohelos* and *Alkwertatherium*, although this feature is variable in *Nimbadon whitelawi* n.sp.); this same line divides the crown such that the anterior moiety is longer than the posterior one (as it does in *Alkwertatherium* but in contrast to either dividing the crown into approximately equal lengths or into shorter anterior and longer posterior moieties as it does in *Neohelos*); poorly developed parastyles and metastyles on upper molars (in contrast to species of *Neohelos* but as in some anterior teeth of other zygomaturines such as *P. centralis*).

ETYMOLOGY

Nimba is a northwestern Queensland Aboriginal word (Wanyi language) meaning 'small'; *don* is Greek for 'tooth'. The name alludes to the small molars found in species of this genus and to the fact that the posterior molars do not increase markedly in size from M2 to M4 as they appear to do in the otherwise similar *Neohelos tirarensis*.

Nimbadon lavarackorum n.sp.
(Figs 2,3)

HOLOTYPE

The holotype is QMF23141, a left maxillary fragment containing M^2, M^3 and the buccal half of P^3.

ETYMOLOGY

The species is named after Sue and Jim Lavarack in recognition of their invaluable support in the field at Riversleigh and as founding members and hard working Councillors of the Riversleigh Society, a support group for Australian palaeontological research.

TYPE LOCALITY AND AGE

Henk's Hollow Locality (Archer & Flannery, 1987) occurs within the sequence of Tertiary limestones outcropping on Riversleigh Station, northwestern Queensland (Archer & Hand, 1984; Archer et al., 1989, 1991). It is stratigraphically near the top of the System C sequence as defined by Archer et al. (1989, 1991). This is interpreted to be stratigraphically higher than Site D (System A containing the Riversleigh Local Fauna;

Archer et al., 1991), Microsite (containing the Nooraleeba Local Fauna; Sigé, Hand & Archer, 1982; Hand, 1993) and Gag Site (near the base of System C, containing the Dwornamor Local Fauna; Flannery & Archer, 1984; Hand, 1985; Archer et al. 1991), but is close to (though still above) the level of Two Trees Site (containing the Two Trees Local Fauna Flannery & Archer, 1987). On the basis of its stratigraphic position and stage of evolution comparisons of its fossil mammals (work in preparation), the Henk's Hollow Local Fauna is tentatively interpreted here to be middle Miocene in age (Archer et al., 1989, 1991).

REFERRED SPECIMENS AND THEIR LOCALITIES

QMF23142 from the Henk's Hollow Locality, a left dentary containing P_3-M_5, is tentatively referred to this species, as are the following isolated teeth from Henk's Hollow: QMF23143, a right P^3; QMF23144, a left P^3; QMF23145, a left M^2; QMF23146, a right M^3; QMF23147, a left M^4; QMF23148, a left $?M^4$; QMF23149, a right M^4; QMF23150, a right M^5; QMF23151, a right P_3; QMF23152, a left P_3; QMF23153, a right P_3; QMF23154, a left $?M_2$; QMF23155, a right M_2, and QMF23160, a right M^{2-3}, were collected from the Gag Site of the same plateau, Riversleigh Station.

REFERRED LOCALITIES AND AGES

The stratigraphic relationships of the Henk's Hollow Local Fauna and the Dwornamor Local Fauna are indicated above. At present, both are interpreted to be middle Miocene in age.

SPECIES DIAGNOSIS

This species is distinguished from *Nimbadon scottorrorum* n.sp. from Riversleigh's Fig Tree locality (see below) by its smaller size, relatively longer P^3, better developed hypocone on P^3, less well-developed parastyle on M^3 and probably more elongate posterior upper molars and less well developed postmetacrista but more discrete metastyle on M^2.

It is distinguished from the similar-sized *N. whitelawi* n.sp. by its almost square (rather than rectangular) upper molars.

DESCRIPTION

P^3 is represented by three specimens: a LP^3 from the holotype, QMF23141; an isolated RP^3, QMF23143; and an isolated LP^3, QMF23144. The tooth is widest across the protocone, sharply pinching in anteriorly and smoothly rounding posteriorly. It is subtriangular and is comprised
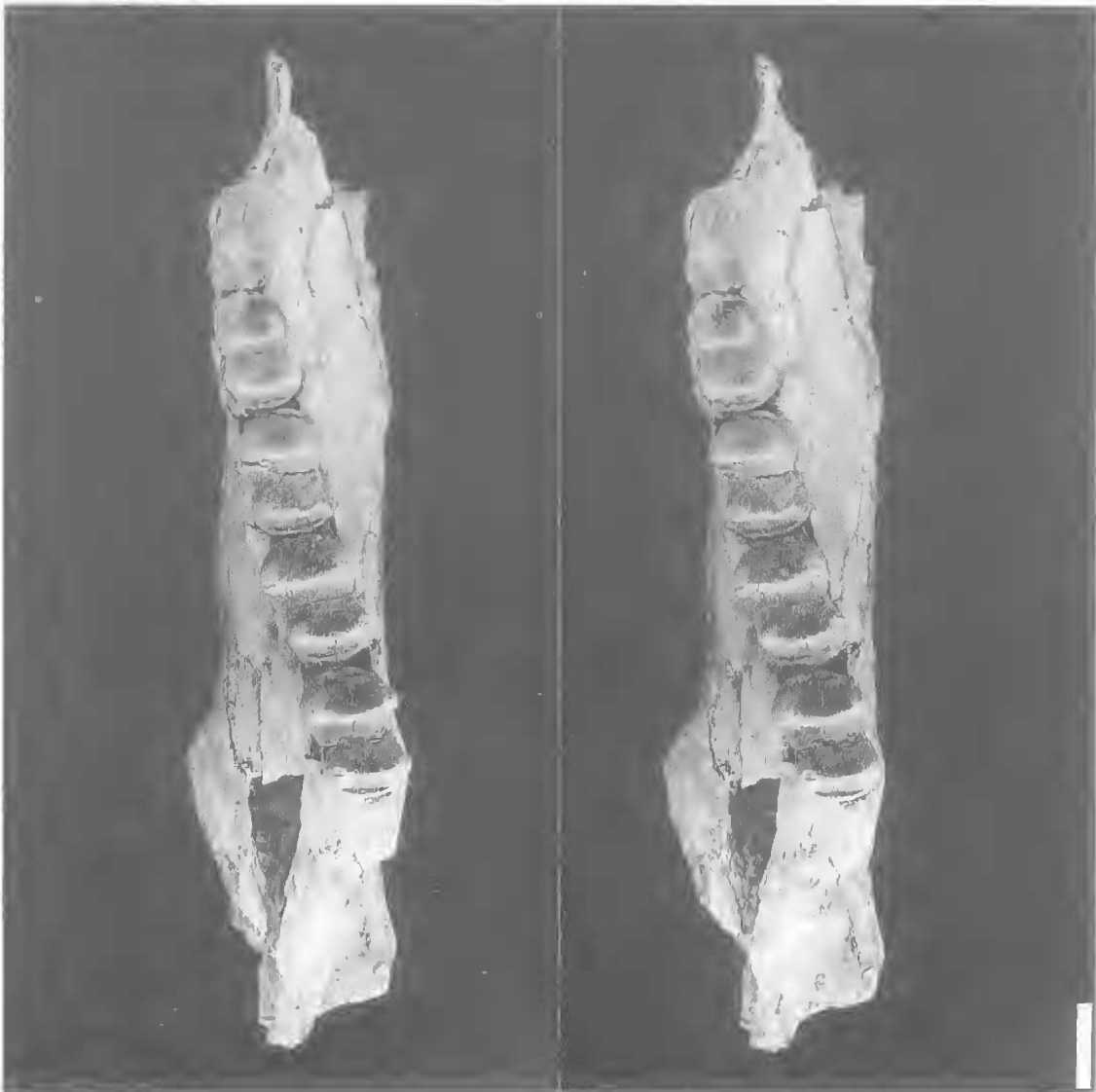
FIG. 3. *Nimbadon lavarackorum* n.gen., n.sp., Henk's Hollow Site, Riversleigh Station. QMF23142, left dentary with P_3, M_2, M_3, M_4 and M_5, occlusal stereopair. Bar indicates 10mm.

of four cusps: the parastyle, parametacone, protocone and hypocone (the latter however being variably developed). The parametacone is the highest cusp. It is blade-like with a strong shearing crest on the posterior edge and a short anterobucally oriented apical crest. The protocone and parastyle are subequal to each other in size. The hypocone is the smallest cusp and is even absent in one specimen (QMF23144). There is no suggestion of a division in the parametacone which is pyramid-shaped having relatively flattened anterior, buccal and lingual faces. The pro-

tocone is lingual to the parametacone and the hypocone lies posterobuccal to the protocone. The hypocone is more sharply separated by deep fissures from the buccal cusps than is the protocone. The parastyle is posteriorly inclined with a short anterolingually oriented apical blade. This large conical cusp forms a strong anterobuccal projection in the occlusal outline of the crown. It is separated from adjacent cusps by a chevron-shaped transverse cleft that is better-developed lingually than buccally. Posterior to this cleft, and on the anterior flank of the parametacone, a con-

spicuous ridge extends anterolingually from the tip of the parametacone to the anterolingual cingulum at a point anterobuccal to the base of the protocone. From the tip of the protocone, a poorly-defined transverse crest runs buccally until it almost meets (but does not) the parametacone ridge, its counterpart, at the commisure that separates the protocone and parametacone. Anterolingually, a very poorly developed (to ?absent) cingulum extends from the anterobuccal base of the protocone to the lingual base of the parastyle but does not continue up the flank of the parastyle. A cingulum is also developed posterobuccally from the buccal flank of the parametacone to the most posterior point of the crown (but is better-developed in some specimens than in others) and appears to be developed posterolingually from this point to at least the base of the hypocone. There is no evidence of an anterobuccal cingulum. From the tip of the parametacone, a prominent crest runs to the posterior margin of the tooth, dividing the posterolingual and posterobuccal cingula. A small crest runs posteriorly from the tip of the protocone to a swelling or cuspule. Another thin crest on the posterior face of the hypocone appears to converge with the posterolingual cingulum (at least in QMF23144). The tooth is two-rooted. The anterior root is conical and slightly anteriorly sloping; the larger posterior root is anteroposteriorly flattened and anteriorly convex. Many of the medial surfaces of the four crowns are covered in fine, poorly developed crenulations. There are two roots: one anterior oval one beneath the parastyle; and a much longer anteroposteriorly compressed root that extends transversely beneath the whole width of the posterior part of the crown.

M^2. The first upper adult molar is known from the holotype, QMF23141, and ?an isolated left M^2, QMF23145. It is a low-crowned almost square transversely lophodont tooth that is only slightly longer than wide. It is comprised of an anterior moiety, the protoloph, and a posterior moiety, the metaloph. Both are anteriorly convex. The paracone and metacone are similar in size as are the slightly shorter protocone and metaconule. The metaconule is slightly higher than the protocone and more lingually-situated. The metaloph is thus wider than the protoloph. The paracone and metacone are slightly closer together than are the protocone and metaconule. In the anterobuccal corner of the tooth a weak parastyle is developed at the buccal end of the short anterior cingulum. There is no metastyle although there is a prominent postmetacrista that extends from the

tip of the metacone to the posterior cingulum with which it merges. A weakly developed postparacrista on the posterior flank of the paracone extends toward the midvalley but stops short of contacting similar premetacristae that extend from the metacone and from just lingual to the metacone towards the midvalley. From the protocone and metaconule, wide but very faint crests extend posterobuccally across the posterior flanks of the protoloph and metaloph. From the protocone, this crest extends to the transverse valley near the midline; from the metaconule this crest extends to the posterior cingulum also near the midline of the tooth.

Wear facettes on these crests exhibit polish and parallel striations (particularly in QMF23145) suggesting that their function was maintained by thegosis against (respectively) the entoconid of M_2 and the metaconid of M_3. The anterior cingulum extends from the parastyle around the lingual base of the protocone where it is interrupted and then continues across the lingual end of the transverse valley to the anterolingual base of the metaconule where it is interrupted and then continues around to the metastyle. There is no buccal cingulum. The M^2 may have been three-rooted with a cylindrical root beneath the paracone and another beneath the protocone and a single wide root beneath the metaloph. Precise thegotic facettes occur on the anterior trailing edges of the protoloph and metaloph blades. The anterior flanks of the protoloph and metaloph are "hollow-ground" in anticipation of the thegotic sharpening of the blades. Fine vertical crenulations on the flanks of the protoloph and metaloph produce secondary, vertical ?beta thegotic blades as the tooth sustains abrasive and thegotic wear.

M^{3-5}. M^{3-5} are similar to M^2 in basic morphology but are slightly larger and higher-crowned. The paracone is larger and more buccally- situated than the metacone. The protoloph and metaloph increase slightly in width from M^{2-4}. The parastyle and postmetacrista are markedly reduced in M^{3-5} such that in M^3 they are represented by terminal swellings in the anterior and posterior cingula respectively and are absent in M^4 and M^5. In some specimens (e.g. M^3 in QMF23160), however, there is a very tiny cuspule on the posterior flank of the metacone of posterior molars. The postparacrista is less well-developed as are the crests from the protocone and metaconule. The mesostyle appears to be lacking. The part of the crown anterior to the protoloph is shorter and the swelling in the transverse valley better developed. The metaloph is much more strongly curved in

M^{3-5} and is more lingually offset with respect to the protoloph.

Dentary. QMF23142, a dentary containing P_3, M_{2-5}, is tentatively referred to this species. It is of a size appropriate for some of the referred upper molars of this species and in its suite of plesiomorphic zygomaturine features (e.g. its lack of a posteriorly increasing molar size gradient), is analogous to the phylogenetic state of the upper molars of *N. lavarackorum.* However, because the specimen appears to be approximately 10% larger than the holotype, there is still some slight doubt about the propriety of referring this dentary to *N. lavarackorum.*

The dentary is badly fractured and is missing the incisor, medial symphysis, angle and ascending ramus. It is deepest below the hypolophid of M_4. The ventral border slopes posteriorly upward from this point and anteriorly upward to at least the hypolophid of M_2. The anterior edge of the coronoid process leads posterodorsally from the body of the horizontal ramus. The postalveolar process is missing. There is no distinct digastric fossa and the area beneath the leading edge of the coronoid process is smooth suggesting that the masseteric fossa was not deep. The mental foramen is located approximately 4mm in front of a vertical line marking the most anterior edge of the P^3 crown. It is round in lateral view and opens anterodorsally onto the buccal surface of the diastemal region. Although the mandibular foramen is not preserved, the mandibular canal is represented by a sulcus at about the level of the tooth row.

The P_3 is preserved in QMF23142 as well as QMF23152, an isolated LP_3, QMF23153, an isolated RP_3 and QMF23151, an isolated RP_3. The tooth is longer than it is wide and more narrow anteriorly than posteriorly. It bears a central principal cusp, the protoconid, and a much smaller medially positioned posterior cingular cusp. These are joined by a prominent longitudinal shearing crest that also extends anteriorly from the protoconid to terminate as a cuspule or cingular swelling at the anterior edge of the crown. Lingual to the principle central cusp there is a variably distinguished cuspule (stylid or vertical cristid). This structure is the apex of a vertical flanking crest that extends ventrally to a point just posterior to the lingual base of the protoconid. This crest is most conspicuous in posterior view. A posterolingual cingulum leads posteriorly from the base of this crest to the base of the posterior cusp. A similar but much less well-developed vertical cristid extends ventrally from the buccal

apex of the protoconid. Taken together, these flanking cuspules and their associated vertical cristids comprise a transverse structure that intersects the crown at its apex at right angles to the main longitudinal shearing cristid. The posterior cingulum is much better developed than the anterior cingulum which is present only at the anterolingual tip of the crown. The posterior cingulum extends from the lingual base of the protoconid to the posterior cuspid where it is met by the buccal base of the protoconid but is best developed in the region of the posterior cuspid where it is met by the main longitudinal crest of the crown. In this area of intersection, the posterior cingulum is conspicuously crenulated in some specimens (i.e. QMF23152 and QMF23153) and slightly less so in others (i.e. QMF23151). In QMF23152, a wear facette on the posterobuccal cingulum, possibly produced by the P^3 parametacone, is developed which is not seen in other specimens. In this same specimen, just anterior to the crenulated posterior cingulum, a transverse crest extends anterolingually from the tip of the posterior cusp to the posterolingual cingulum. In all specimens, a wear facette for M_2 is developed at the tallest point of the posterior cingulum. The tooth is double-rooted, the anterior root being conical in shape, the posterior root being anteroposteriorly flattened.

Specimens QMF23152 and QMF23153, although similar in morphology, are considerably smaller than the P_3 preserved in the dentary. The P_3 in this species might be sexually dimorphic.

M_2. The M_2, known from QMF23142 and QMF23154? (and the Gag Site QMF23155), is an elongate, subrectangular tooth that is narrower anteriorly than posteriorly. The trigonid of M_2 is represented by a transverse protolophid and an arcuate anterolingually directed paracristid that extends to the anterior margin of the tooth. From the protoconid a short indistinct crest (?protocristid) appears to extend posterobuccally to terminate in a slight swelling which is perhaps the protostylid. From the metaconid, a crest extends anteriorly a short distance. From the entoconid, a short entocristid extends anterolingually.

In occlusal view, the paracristid is convex buccally, the protolophid is transverse or very slightly posteriorly convex and the hypolophid is markedly posteriorly convex. The protolophid is narrower than the hypolophid. An anterior cingulum is present both buccal and lingual to the anterior end of the paracristid. The cingulum on the buccal side is not preserved in QMF23142, is distinct (between the protolophid and hypolo-

phid) in QMF23155 but not in QMF23154. There is no lingual cingulum or cristid obliqua in QMF23142 but there is a lingual cingulum in QMF23155 (again between the protolophid and hypolophid). The posterior cingulum connects the posterior base of the hypoconid to that of the entoconid. A wear facette is developed at the midpoint of the posterior cingulum. Distinct wear facettes extend along the posterior lengths of the protolophid and hypolophid. In lingual view, the floor of the transverse valley is U-shaped. The protoconid is taller than the subequal metaconid, hypoconid and entoconid. The tooth is double-rooted but these are not well preserved in the isolated teeth QMF23154 and QMF23155.

QMF23154 (M_2?) has a paracristid and pre-metacristid that are much less distinct than those preserved in the dentary and Gag Site specimen. Only the paracristid extends to the anterior cingulum of the tooth. In this specimen, the enamel on the posterior face of the protolophid has prominent vertical crenulations. The cristid obliqua is also distinct although low and extends as a minor vertical crenulation on to the posterior flank of the protolophid.

M_{3-5}. Unlike M_2, trigonids of the posterior molars lack a prominent paracristid and are more rectangular in appearance with the protolophid being slightly wider than the hypolophid in M_{3-5}.

In M_3, the protolophid and hypolophid are approximately the same width. The paracristid forms a poorly-defined vertical crest that extends only partly down the anterior face of the protolophid. The premetacristid is also poorly defined and extends approximately the same distance. Protolophids and hypolophids become more posteriorly convex from M_2 to M_5. In M_{4-5}, the protolophids are markedly wider and the hypolophids are lingually displaced. M_4 and M_5 are larger than M_3.

Nimbadon whitelawi n.sp.
(Fig. 4)

HOLOTYPE
The holotype and only known specimen is NMVP186506. It preserves the palate, RP^3-M^5 and LP^3-M^3. All teeth except LP^3 are damaged and LM^3 and RM^5 are missing parts of their posterior halves.

ETYMOLOGY
This species is named after Michael Whitelaw who assisted in the collection and processing of specimens from Bullock Creek.

TYPE LOCALITY AND AGE
The type locality is fossil vertebrate locality WV 113 in Bultitude (1973) (17°7'S, 131°32'E), the Horseshoe West locality of the Camfield Beds at Bullock Creek, Camfield Station, northwestern Northern Territory. The Bullock Creek Local Fauna (Plane & Gatehouse, 1968; Archer & Bartholomai, 1978; Rich et al., 1991; Archer & Hand, 1984; Murray & Megirian, 1990, 1992) is currently interpreted to be ?middle Miocene, i.e. immediately post-Wipajiri, in age (Woodburne et al., 1985; Murray, 1990a; Murray & Megirian, 1990, 1992).

SPECIES DIAGNOSIS
This species is distinguished from *N. lavarackorum* and *N. scottorrorum* by its markedly more elongate (i.e. less square) upper molars and relatively more anteriorly situated buccal swelling on P^3. It is also distinguished from *N. scottorrorum* by its relatively much longer P^3 and markedly convex anterior and posterior molar crown margins such that these teeth have a much reduced area of interdental contact.

DESCRIPTION
The species is described insofar as it differs from *Nimbadon lavarackorum*.

The palate preserves most of the right and a large part of the left maxillae and small fragments of the left and right palatines. Anteroventrally, the palate is fractured at or behind the premaxillo-maxillary suture. Posteroventrally, it preserves the maxillo-palatine suture. The latter extends anteriorly to a point medial to the posterior part of M^3. Palatal ridges extend longitudinally and anteriorly along the length of the palate from the level of M^3. The right diastemal crest runs anterolingually. The tooth rows are parallel to slightly convex buccally. Anteriorly, doming of the median region of the palate is marked. It extends posteriorly to the level of the rear of M^2 and, though shallowing perhaps, anteriorly to at least just behind the premaxillo-maxillary boundary. There is a pair of nutrient foramina on the right side of the palate medial to P^3 and on the left side a single foramen. Medial to the hypoloph of M^2, is another tiny foramen on each side of the palate. The infraorbital foramen canal is about 30mm in length. The infraorbital canal opens onto the face 14mm above the anterior edge of the P^3 alveolus. Sutural relationships of the palatine, lacrimal, jugal and maxillary bones are unclear. There is no evidence for maxillary or palatal vacuities although the anterior and posterior ex-
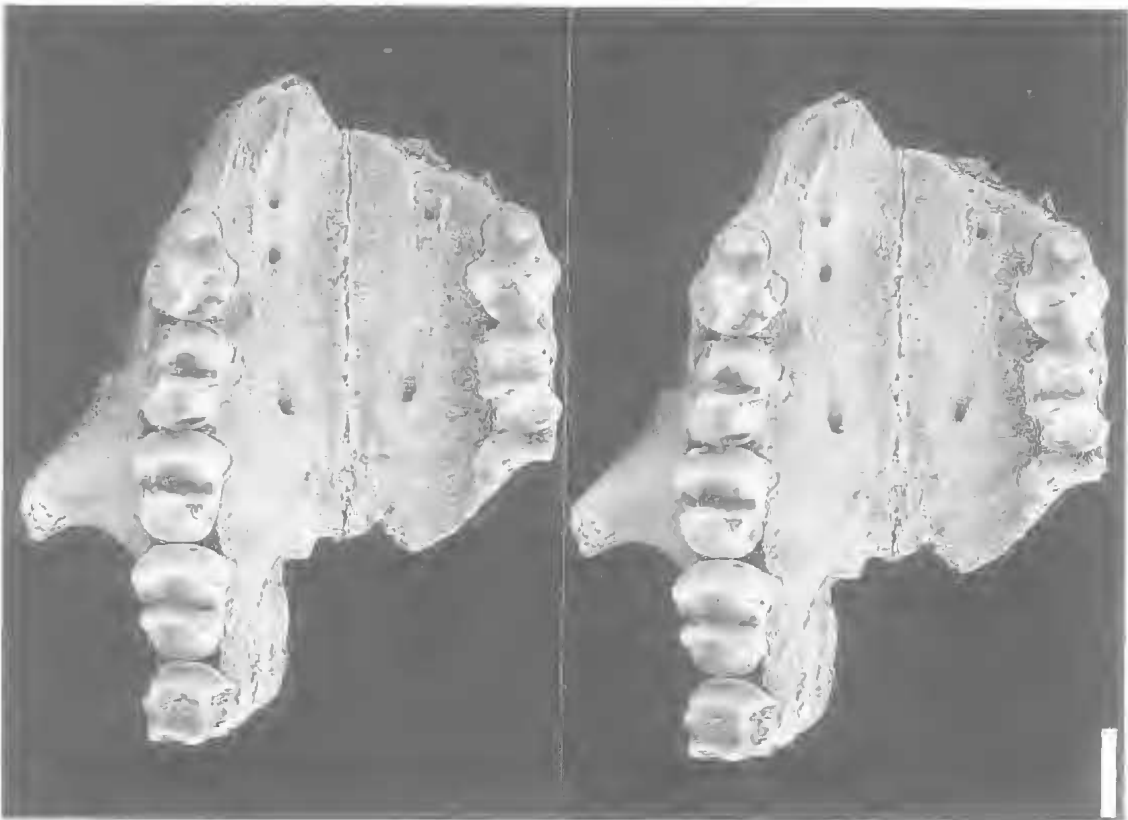
FIG. 4. *Nimbadon whitelawi* n.sp., Bullock Creek, Northern Territory. NMVP186506, palate with RP^3-M^5 and LP^3-M^3, occlusal stereopair. Bar indieates 10mm

tremities of the palate are missing. The maxillary process near the roof of the zygomatic arch, although damaged, is down-turned and conspicuous but does not extend ventrally below the level of the palate. There appears to have been a very reduced orbital wing of the maxilla, although bone boundaries in this region are unclear.

Upper dentition. The P^3 differs from most specimens (all except QMF23144 AR5513) of *N. lavarackorum* in the greater degree of devclopment of the hypocone. In *N. whitelawi* the parastyle appears to be less posteriorly inclined and the anterolingually-directed crest that extends from the parametacone to the anterolingual cingulum is less distinct although it is possibly diminished by wear. It nevertheless approaches the buccal crest from the protocone at a steep angle rather than perpendicular.

The M^2 on both sides of the holotype is damaged buceally and lingually. However, it appears to differ from both Riversleigh species of *Nim-*

badon in being longer relative to P^3 and in appearing to be rectangular rather than square.

The M^3 appears to differ from the Riversleigh species in a similar way as M^2, but it appears to be relatively even more elongate. M^2 and M^3 are approximately cqual in length.

The M^4 differs less from that tooth in the other species of *Nimbadon*.

All of the cheekteeth of *N. whitelawi* appear to differ from those of *N. scottorrorum* in having anteriorly and posteriorly markedly convex tooth margins so that the crowns abut with limited contact.

Nimbadon scottorrorum n.sp.
(Fig. 5)

HOLOTYPE
The holotype and only known specimen is QMF23157 (formerly SAMP27815), a right maxillary fragment containing P^3, M^2, M^3, M^4 and M^5. While P^3 and M^2

are intact, M^{3-5} are missing the buccal margins of the crown.

ETYMOLOGY

The species is named after Sue and Don Scott-Orr, in recognition of their long-term support for the Riversleigh Palaeontological Research Project. With the Lavaracks, they are also founding members and Councillors of the Riversleigh Society.

TYPE LOCALITY AND AGE

The type locality, Fig Tree Site, is adjacent to Godthelp Hill, Riversleigh Station, northwestern Queensland. It is laterally adjacent to units regarded by Archer et al. (1989, 1991) to be part of System B although it may actually be from the basal part of System B or even upper part of System A, hence stratigraphically below Henk's Hollow (upper part of System C; Archer, Hand & Godthelp, 1986) and Gag Site (lower part of System C; Flannery & Archer, 1984; Hand, 1985) and possibly above or equivalent to Microsite (?System A; Sigé, Hand & Archer, 1982; Archer et al., 1989, 1991) and Site D (System A; Tedford, 1967; Archer et al., 1989, 1991). On this basis and stage of evolution comparisons of the marsupials in these faunas, the Fig Tree Local Fauna is interpreted to be ?late Oligocene-early Miocene in age.

SPECIES DIAGNOSIS

This species is distinguished from *Nimbadon lavarackorum* and *N. whitelawi* by its larger size, anteroposteriorly compressed P^3 (which is much shorter than any upper molar), its more robust cingula on all cheekteeth and its greater parastylar development in M^{2-3} (contributing to the squared appearance of these teeth). It also has less convex anterior and posterior molar crown margins which therefore have much wider interdental contact with each other.

It is further distinguished from most (but not all) *N. lavarackorum* by its much smaller hypocone on P^3.

DESCRIPTION

Nimbadon scottorrorum differs from *N. lavarackorum* and *N. whitelawi* as follows:

The P^3 is markedly anteroposteriorly compressed such that it is almost as wide as it is long

and is subrounded in shape. Unlike *N. lavarackorum*, in which P^3 is equal in length or longer than any adult upper molar, in *N. scottorrorum* this tooth is the shortest in the tooth row. The hypocone appears to have been very poorly developed.

The anterobuccal corner of M^2 has a much squarer appearance due to greater parastylar development in the anterior cingulum. This is true also of the posterobuccal corner of the tooth where metastylar development occurs mid-way along the postmetacrista.

Parastylar development in M^3 is relatively marked compared with its condition in *N. lavarackorum*. The teeth are buccally fractured in M^{3-5} making it impossible to determine the degree of development of the buccal cusps in M^{4-5}.

DISCUSSION

The three diprotodontids described here appear to comprise a new clade of zygomaturines. As species of the new genus *Nimbadon*[1], they may be distinguished from other zygomaturines by, among other features, a combination of upper premolar attributes. Premolar morphology was extensively used by Stirton (1967) and Stirton et al. (1967) to help resolve distinctions between diprotodontid lineages and has subsequently been used by most workers. Few other character systems have been found to be as useful in distinguishing probable inter-relationships among Tertiary diprotodontids.

Since Stirton et al.'s (1967) review of Tertiary diprotodontids, diverse diprotodontoid materials have been collected from Oligo-Miocene fossil sites at Riversleigh, Bullock Creek, Alcoota and Beaumaris and from Pleistocene sites in New Guinea (e.g. Flannery, 1992) and many areas of Australia. This material includes specimens representing new genera and probably new diprotodontoid subfamilies. Murray (1986, 1990a,b) has named several new Tertiary taxa but the bulk of the material, particularly from Riversleigh sites, is yet to be described. As a result of the new discoveries, the superfamily Diprotodontoidea is in need of major revision.

At present (e.g. the reviews of Archer, 1984; Aplin & Archer, 1987; Marshall, Case & Woodburne, 1989; Murray, 1990b) two diprotodontoid families are recognised: the Palorchestidae; and the Diprotodontidae with two subfamilies, the

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[1] The generic name *Nimbadon* was used by Murray (1990b) in a cladogram of hypothetical phylogenetic inter-relationships among Miocene diprotodontids. However Murray did not designate a species of *Nimbadon* in the cladogram or in the ensuing discussion, and, as outlined in Article 13B of the Code of Zoological Nomenclature, '*Nimbadon*' was thus used as a *nomem nudum*.
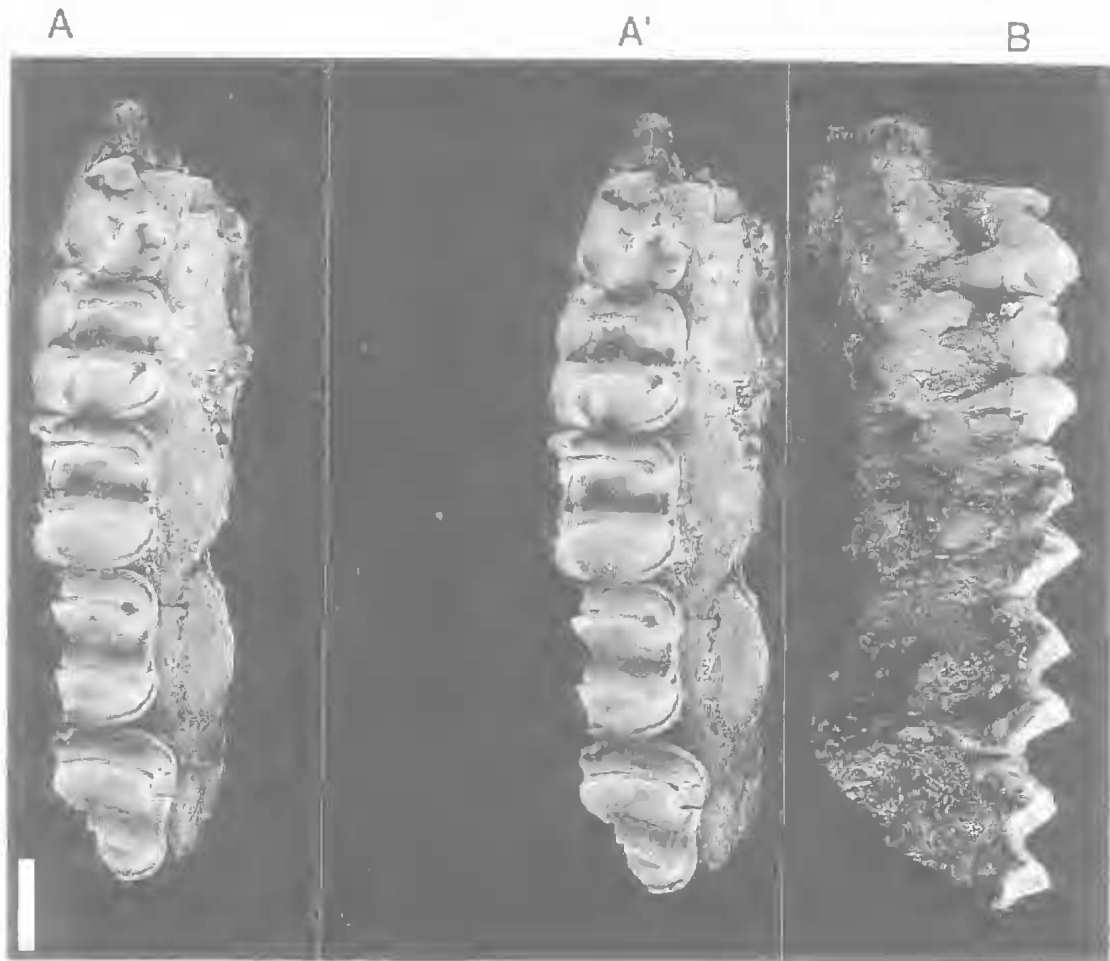
FIG. 5. *Nimbadon scottorrorum* n.sp., Fig Tree Site, Riversleigh Station, QMF23157, right maxillary fragment with RP^3- M^5, A-A', occlusal stereopair; B, buccal view. Bar indicates 10mm.

Diprotodontinae and the Zygomaturinae. Although zygomaturines have traditionally (e.g. Stirton et al., 1967) been considered to be among the most primitive of diprotodontoids, it is by no means certain that this is so (Murray, 1990b). It is not clear what might be used as an appropriate outgroup in a phylogenetic analysis of zygomaturines nor, consequently, are polarities of character state morphoclines within the Zygomaturinae confidently determined.

Murray (1990b) has discussed other difficulties in analysing diprotodontid phylogenetics. He notes that despite the fact that many Tertiary diprotodontids are represented by almost-complete skull and dentary material, discontinuities in some character complexes and the continuously varying nature of others tend to obfuscate clarification of relationships between taxa. Con-

siderable variability in cranial morphology has been observed in some zygomaturines (e.g. in a *Neohelos* sample from the Bullock Creek Local Fauna; P. Murray, pers.comm.), and the molar dentitions of the zygomaturines *Plaisiodon centralis* Woodburne, 1967 and *Alkwertatherium webbi* Murray, 1990b and the diprotodontine *Pyramios alcootense* Woodburne, 1967 have been found to overlap in size and morphology (Murray, 1990b).

It is perhaps a measure of the difficulties encountered in determining species and generic boundaries for diprotodontids that *Nimbadon* is one of few non-monotypic Tertiary zygomaturine genera, the others being *Kolopsis* Woodburne, 1967 and *Zygomaturus* Owen, 1859.

Recognition of the genus *Nimbadon* has been facilitated by re-diagnosis of *Neohelos* Stirton,

1967 based on new material obtained by Archer and colleagues 20 years after the original material was collected by Stirton and colleagues from the Leaf Locality of Lake Ngapakaldi, South Australia. This provides novel information about the anterior morphology of P^3, which exhibits, among other distinctive features, a large, erect parastyle. This feature is also present in specimens referred to *Neohelos* from the Bullock Creek and Riversleigh Tertiary faunal assemblages (Plane & Gatehouse, 1968; Plane, 1971; Rich et al., 1982; Murray & Megirian, 1990, 1992; Archer et al., 1989, 1991).

In his review of Oligo-Miocene diprotodontid taxa, Murray (1990b) postulates a number of phylogenetic hypotheses, only one of which is expressed in his cladogram (fig. 14). The latter is based primarily on analysis of dental characters (in particular, P^3), using species of the Oligo-Miocene palorchestid genera *Ngapakaldia* and *Pitikantia* as outgroups. In it, Murray identifies species of *Kolopsis* and *Zygomaturus* as the most derived diprotodontids and *Neohelos tirarensis* as their closest relative. Species of *Nimbadon* form the sister-group to the *Neohelos–Kolopsis–Zygomaturus* clade, with *Plaisiodon centralis* being the sister-group of a *Nimbadon–Neohelos–Kolopsis–Zygomaturus* clade, *Kolopsoides cultridens* Plane, 1967 the sister-group of a *Plaisiodon–Nimbadon–Neohelos–Kolopsis–Zygomaturus* clade and *Alwertatherium webbi* the most plesiomorphic of zygomaturines. Species of *Pyramios, Euryzygoma, Bematherium* and *Diprotodon* form a separate (diprotodontine) clade. *Raemeotherium yatkolai* Rich, Archer & Tedford, 1978 from the ?late Oligocene Namba Formation of Lake Pinpa, South Australia, is interpreted to be the most plesiomorphic member of the family Diprotodontidae.

On the basis of his broader study of dental and cranial characters, however, Murray (ibid.) concludes that there are probably two minor zygomaturine lineages: one represented by species of *Nimbadon, Neohelos* and *Kolopsis,* a group he suspects may consist of taxa related largely by symplesiomorphies; the other lineage possibly containing species of *Alwertatherium, Plaisiodon* and *Kolopsoides,* although for this clade he can find even less concrete evidence. He suggests that these two lineages might be related through common ancestry in *Nimbadon.* He also suggests in the text, but not the cladogram, that *Nimbadon* species could represent basal zygomaturines with some specific affinity to *Plaisiodon centralis* and *Neohelos tirarensis,* and that *Plaisiodon centralis*

is more closely related to *Alkwertatherium webbi* than to any other zygomaturine.

A phylogenetic hypothesis of diprotodontid inter-relationships, including the three new *Nimbadon* species and broadly based on Murray's cladistic analysis of dental characters, is given in Fig. 6. The polarity of some characters has been interpreted differently from Murray (1990b) but basic intergeneric relationships remain unchanged except for the position of *Plaisiodon centralis.*

In Fig. 6 and Murray (1990b), the Zygomaturinae are clustered on the basis of a large parastyle on P^3 which is separated from the parametacone by a deep cleft. The *Kolopsoides-Plaisiodon-Nimbadon-Neohelos-Kolopsis-Zygomaturus* clade shares as a synapomorphy development of a hypocone in P^3. The basic proportions of P^3 are apomorphically shared by species of the *Nimbadon, Plaisiodon, Neohelos* and Kolopsis clade (but see Murray, 1990b), with a division in the parametacone interpreted to have occurred subsequently in the *Kolopsis* lineage. Retraction of the mesostyle towards the cingulum in P^3 clusters species of *Neohelos* and *Kolopsis* (Murray, 1990b).

In both cladograms, the posteriorly inclined (or hooked) parastyle of P^3 in species of *Nimbadon* is regarded to be apomorphic. Only one other zygomaturine exhibits this feature — *Plaisiodon centralis.* Although species of *Nimbadon* are readily distinguished from *P. centralis* by aspects of upper premolar morphology (including in *P. centralis* the very large hypocone and the lingual crest from the parametacone linking to the protocone rather than the anterolingual cingulum) as well as by their small size, lack of a posteriorly increasing molar gradient and absence of metalophids on lower molars, sharing of the distinctively shaped parastyle may indicate an albeit distant phylogenetic relationship.

Although the three taxa described here as species of *Nimbadon* may, when better known, prove not to be monophyletic, all exhibit the distinctive crest on P^3 running lingually from the parametacone to the protocone then anteriorly to the anterolingual cingulum, a feature not previously noted in any other diprotodontoid taxa. Other features that characterise the new taxa include their small size and an $M_2:M_4$ length ratio which approaches 1.0. The latter are interpreted here and generally (see below) to be plesiomorphic features among diprotodontids, but they might equally be interpreted to represent apomorphic reversals within certain zygomaturine lineages.
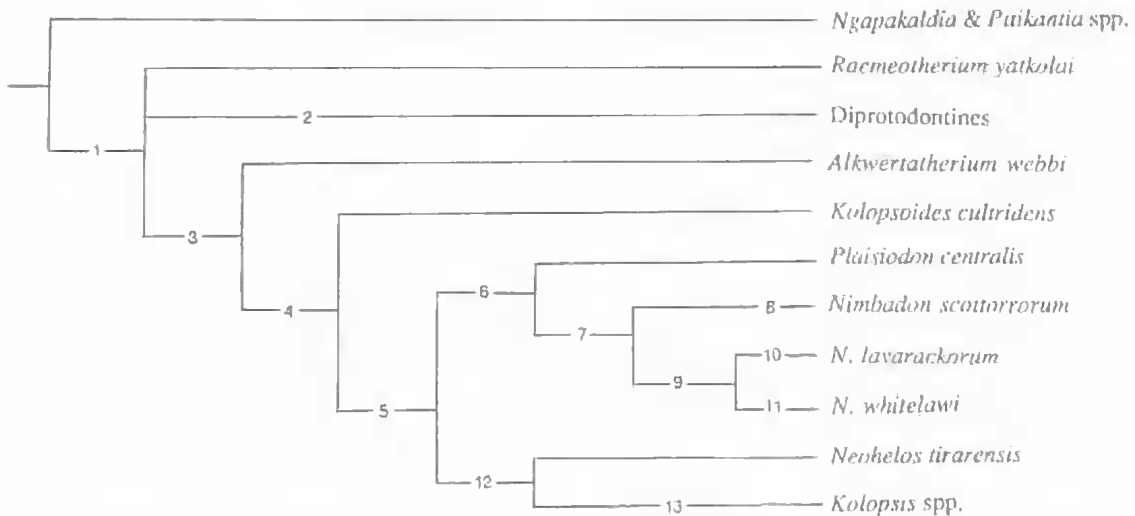
FIG. 6. A phylogenetic hypothesis of zygomaturines, broadly based on Murray's (1990b) cladistic analysis of dental characters in the Diprotodontidae. Apomorphies are as follows: 1, loss, incorporation or suppression of stylar cusps C and D with respect to the lophs on upper molars; 2, reduction of paralophid crest on M_2; 3, large parastyle on P^3 separated from parametacone by a deep cleft; 4, development of a hypocone on P^3; 5, basic proportional similarity of P^3; 6, hooked parastyle on P^3; 7, apical blade and diagonal crest on P^3; 8, shortening of P^3; 9, elongation of posterior molars (i.e. at least M3-4); 10, hypertrophy of P^3 hypocone; 11, elongation of anterior molars, i.e. M2; 12, mesostyle on P^3 retracted towards cingulum; 13, division in P^3 parametacone.

We can, however, find no pressing evidence to closely align individual species of *Nimbadon* with any previously known zygomaturine taxa.

Most zygomaturines — including species of *Zygomaturus*, *Kolopsis*, *Kolopsoides* and *Plaisiodon* — exhibit a marked increase in molar size from M2 to M4 (with an M_2-M_4 length ratio of 0.85 or less) with M5 generally decreasing in size (see also Rich, Archer & Tedford, 1978). Whether this is also true of topotypical *Neohelos tirarensis* is not known but *Neohelos* specimens from Bullock Creek and most from Riversleigh exhibit this feature.

A molar gradient of M2:M4 length approaching 1.0 is regarded by Rich, Archer & Tedford (1978) to be plesiomorphic in zygomaturines. *Raemeotherium yatkolai*, commonly considered to be the most primitive of known zygomaturines (but see Murray, 1990b, and below) and represented by a dentary, isolated lower teeth and an upper incisor from the Oligo-Miocene Namba Formation of Lake Pinpa, also has uniformly sized molars (with a ratio of M_2:M_4 length of 0.96). Palorchestids and diprotodontines variably exhibit this feature and one of the oldest known diprotodontoids, represented in the early Miocene Geilston Bay Local Fauna by a maxilla preserving part of M^2 and M^3, also has uniformly sized molars. The latter is similar in size to *R.*

yatkolai but is tentatively considered by Tedford et al. (1975) to be a palorchestid. Apart from its slightly larger size, *Nimbadon lavarackorum*, the only species of the genus so far represented by lower molars, like all other zygomaturines differs from *R. yatkolai* in its reduction of anterior entocristids. *Nimbadon* species further differ from *Raemeotherium yatkolai* in being larger; in having a more massive dentary which, in transverse width, is approximately twice the width of M_3; in having less well developed cristids obliqua; relatively wider trigonids on all molars; trigonid of M_2 nearly the same width as the talonid (in contrast to *R. yatkolai* where it is markedly narrower); metaconid of M_2 as high as the protoconid and associated with a prominent, steeply inclined, swollen anterior buttress; metacristid of M_2 transversely oriented (in contrast to *R. yatkolai* where it is posterobuccally oriented); "arcuate" (rather than anteroposteriorly rectilinear) paracristid on M_2; and lophids of lower molars less occlusally concave.

It is possible that molar size gradients in zygomaturines are allometrically related to body-size, with larger animals exhibiting relatively larger posterior molars. From Oligo-Miocene deposits on Riversleigh Station, small diprotodontines have been found with M2:M4 length gradients approaching 1.0. Equally, however, the

larger of the Riversleigh species of *Nimbadon* described here (*N. scottorrorum*) appears to have been similar in overall size to at least one undescribed Riversleigh *Neohelos* that shows a marked progressive increase in molar size from M2 to M4. It seems, therefore, that the feature is not always dependent on absolute size although it may vary allometrically within lineages. In Fig. 6 it has been interpreted to be autapomorphic within various clades.

Intrageneric relationships within *Nimbadon* are not much easier to interpret. *Nimbadon whitelawi* differs from both *N. lavarackorum* and *N. scottorrorum* in its markedly more elongate upper molars (particularly with respect to *N. scottorrorum*) and relatively more anteriorly situated buccal swelling on P³. *Nimbadon lavarackorum* differs from *N. scottorrorum* in its smaller size, less well-developed parastyle on M³ and probably more elongate posterior upper molars and less well developed postmetacrista but more discrete metastyle on M². *Nimbadon scottorrorum* is larger than both *N. lavarackorum* and *N. whitelawi*, has more robust cingula on all cheek-teeth and greater parastylar development in M²⁻³ (contributing to the squared appearance of these teeth). Within *Nimbadon*, features such as the hypertrophy of the P³ hypocone in some specimens of *N. lavarackorum* and the shortening of P³ in *N. scottorrorum* appear to be autapomorphic features unique to those species. The most striking differences between the taxa lie in the degree of squaring (or conversely elongation) of the upper molars.

There are two quite different phylogenetic interpretations of *Nimbadon* species, depending on whether elongation (versus squaring) of the upper molars is considered to be plesiomorphic or apomorphic. Commonality would indicate squared upper molars to be plesiomorphic among diprotodontian marsupials including phalangeridans, vombatimorphians and even plesiomorphic kangaroos. However, within the Diprotodontidae the otherwise 'plesiomorphic' (i.e. simple) *Raemeotherium yatkolai* has relatively elongate lower molars and, although no uppers molars are yet known, they too would probably have been relatively elongate, using as a guide the relative proportions of the upper and lower molars of *N. lavarackorum*. It should be noted that the presumption that *R. yatkolai* is the most plesiomorphic diprotodontid is based on its simplicity. Simplicity, however, often characterises the smaller members of some diprotodontian lineages (e.g. pseudocheirids and macropodids) and

all members of other lineages with ubiquitously small members (e.g. burramyids and acrobatids).

Because so few dental character systems have been found to be useful in diprotodontid systematics, polarity swings of this kind greatly influence the interpreted relationships of taxa and their biostratigraphic significance. If elongation is plesiomorphic among diprotodontoids, then *N. whitelawi* would be the most plesiomorphic of the three *Nimbadon* species. Its presence in the middle Miocene Bullock Creek Local Fauna and the presence of what would then be interpreted to be the most apomorphic in the older Fig Tree Local Fauna, would not be support for the currently understood stratigraphic relationships. If, on the other hand, elongation is interpreted to be apomorphic, then the most derived species (*N. whitelawi*) occurs in one of the younger faunas and the most plesiomorphic (*N. scottorrorum*) in the oldest of the faunas (Fig Tree).

The stratigraphic relationships of the fossil assemblages have been discussed in the Systematics section above. The Fig Tree Site occurs adjacent to units regarded to be part of Riversleigh's System B sequence as defined by Archer et al. (1989, 1991), though it may actually be basal System B or upper System A, and is interpreted to be late Oligocene to early Miocene in age. The Henk's Hollow Site occurs near the top of Riversleigh's System C sequence and the Gag Site near its base. Both lie stratigraphically above the Fig Tree level. On the basis of their positions and stage of evolution comparisons of their fossil mammals, they are interpreted to be middle Miocene in age and are probably similar in age to the Bullock Creek assemblage. The Bullock Creek Local Fauna has been interpreted by Woodburne et al. (1985), Murray (1990a) and Murray & Megirian (1990) to be middle Miocene, i.e. immediately post-Wipajiri, in age.

On balance, we consider the phylogenetic relationships of *Nimbadon* species (Fig. 6) to approximately correspond to current understanding of the relative ages of the deposits from which the specimens were obtained but conclude that for the moment at least caution is appropriate in attempts to use zygomaturines to correlate northern Australian Tertiary mammal-bearing faunas.

ACKNOWLEDGEMENTS

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